OCCURRENCE OF *COSTACOPLUMA* (DECAPODA: BRACHYURA: RETROPLUMIDAE) IN THE MAASTRICHTIAN OF SOUTHERN MEXICO AND ITS PALEOBIOGEOGRAPHIC IMPLICATIONS

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ABSTRACT

The second report of the retroplumid crab *Costacopluma* in America is documented by the description of *Costacopluma bishopi* n. sp. on the basis of small exuviae, interpreted to be juveniles, in Maastrichtian deposits of Guerrero, southern Mexico. The Mexcala Formation is a flysch-like sequence interpreted to be deltaic sediments deposited at the edge of an eastward accreting margin. Comparison with the three other described species of *Costacopluma* suggests that this genus contains two phyletic groups: one American and one African; however, lack of cuticle in the retroplumids from Guerrero makes it difficult to describe the species fully. The Retroplumidae is considered to contain *Archaeopus*, *Costacopluma, Cristipluma, Bathypluma* and *Retropluma*, the first of which is the oldest known genus within the family. An American origin for the Retroplumidae is proposed, and the presence of *Costacopluma* in the Coniacian–Paleocene of West Africa and the Maastrichtian of North India is explained on the basis of an eastward dispersal from North America. Paleobiogeographic distribution of crabs inhabiting the inner sublittoral during the Late Cretaceous was influenced by paleoclimatic factors. During Maastrichtian time, dakoticancrid crabs were prevalent in the Western Interior and Atlantic and Gulf Coastal Plain shelf decapod assemblages, while in northeastern and southern Mexico, retroplumid crabs were the dominant element. Late Cretaceous regression severely affected shelf benthic communities, resulting in extinction of American retroplumids and a decrease in the African and Indian populations. The remaining few retroplumid representatives radiated into deep water subsequent to Paleocene time. The Indo-Pacific distribution of the nine extant retroplumid species is a relict of a once wider distribution.

INTRODUCTION

Crabs are among the rarest fossils. Often they are inconspicuous in outcrops with high diversity and abundance of other invertebrates. Only rarely do they occur as decapod-dominated assemblages. Frequently they are found accidentally while prospecting for other macrofauna in fossiliferous sequences. Preservational styles and specimen size are unpredictable even when the paleoenvironment of a sedimentary sequence is well understood. Periodic molting generates a relatively large number of exuviae which may be displaced far from where the crab molted. Size distribution of fossils is dependent upon age of the crabs, habitat of juveniles and adults, and energy of the environment. As the crab grows, the chitinous exoskeleton becomes more durable as additional carbonate is incorporated. For this reason, juvenile exuviae tend to be more delicate and their preservation is less likely.

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Fig. 1.—Location map of the area studied in Guerrero, southern Mexico, south of Mexico City.

This paper describes what are interpreted to be juvenile exuviae of the genus *Costacopluma* found in a Maastrichtian terrigenous sequence assigned provisionally to the Mexcala Formation, of Guerrero in southern Mexico (Fig. 1). Paleoenvironmental interpretations and paleobiogeographical implications are suggested as the basis for future paleocurrent and paleogeographic reconstructions for the Maastrichtian in this portion of North America.

Relatively few fossil crabs have been reported from Mexico. The stratigraphically oldest malacostracan from Mexico (Alencaster, 1977) is *Astracodes* sp. cf. *A. maxwelli* Stenzel from the Hauterivian–Aptian (Early Cretaceous) limestones of the San Lucas Formation in Guerrero. Stenzel (1944) reported *Graptocarcinus muiri* Stenzel from the Aptian Taninul Limestone in San Luis Potosi. *Meyeria mexicana* Rathbun was found in the Cuchillo Parado Formation (Aptian) in Chihuahua (Rathbun, 1935). Rathbun (1930) reported *Podophthalmus* (?) sp. from Upper Cretaceous deposits of Villagran in Tamaulipas. Maastrichtian decapods from northeastern Mexico include: *Enoploclytia tumimanus* Rathbun from the Escondido Formation (Rathbun, 1935); *Costacopluma mexicana* Vega and Perrilliat, from the Potrerillos Formation of the Difunta Group (Vega and Perrilliat, 1989); *Dakoticancer australis* Rathbun, and *Mascaranada difuntaensis* Vega and Feldmann, from the Potrerillos Formation (Vega and Feldmann, 1991). *Xandarus sternbergi* (Rathbun) was reported and redescribed as *Zanthopsis sternbergi* (Rathbun, 1926), from the Maastrichtian Rosario Formation of northwestern Mexico,

in Baja California (Bishop, 1988). Tertiary deposits from Jalisco contain the isopod *Sphaeroma burkartii* Barcena (Barcena, 1875; Hessler, 1969). Five Eocene decapods from Baja California were described by Rathbun (1930): *Calappilia hondoensis* Rathbun, *Callianassa tepetatensis* Rathbun, and *Raninia* sp. from the upper Eocene Tepetate Formation; *Lobonotus mexicanus* Rathbun, and *Montezumella tubulata* Rathbun from the upper Eocene beds of Arroyo Colorado. *Harpatocarcinus americanus* Rathbun from Tamaulipas and *Callianassa pustulata* Whiters from Veracruz (Rathbun, 1930) are also Eocene in age. Oligocene deposits from Mexico contain *Xanthosia americana* Rathbun from Tepetate, Baja California; *Scylla costata* Rathbun from an unknown locality; *Calappa zurcheri* Bouvier from Veracruz; *C. flammea* (Herbst) from Tepetate, Baja California (Rathbun, 1930), and *Callianassa vaughani* Rathbun from San Fernando, Tamaulipas (Rathbun, 1935). *Raninoides mexicanus* Rathbun and *Callianassa pellucida* Rathbun were reported from Miocene deposits of Veracruz (Rathbun, 1930).

The Retroplumidae, erected by Gill (1894), includes *Archaeopus* Rathbun, 1908; *Costacopluma* Collins and Morris, 1975; *Cristipluma* Bishop, 1983, *Retropluma* Gill, 1894 (=*Archaeoplax* Alcock and Anderson, 1894 *non* Stimpson, 1863), and *Bathypluma* (Saint Laurent, 1989). The last two are the only extant genera in the family. *Retropluma* and *Bathypluma* are represented by nine species inhabiting Indo-Pacific seas (Saint Laurent, 1989). Late Cretaceous Retroplumidae from North America include *Archaeopus antennatus* Rathbun from the Chico Formation of California (Rathbun, 1908); *A. vancouverensis* Woodward from the Spray Formation of British Columbia (Woodward, 1896); and *Cristipluma mississippiensis* Bishop from lower Maastrichtian deposits of the Coon Creek Formation, Mississippi (Bishop, 1983). *Costacopluma mexicana* Vega and Perrilliat from the upper Maastrichtian Potrerillos Formation in Nuevo Leon, Mexico, is the first report for that genus in America (Vega and Perrilliat, 1989). The description of *Costacopluma* was based on *C. concava* Collins and Morris (1975) from Upper Cretaceous deposits in Nigeria, a species subsequently reported from the Maastrichtian of north India (Gaetani et al., 1983). Collins and Morris (1975) transferred *Archaeopus senegalensis* Remy, from the Paleocene of Senegal, to *Costacopluma.* The oldest record of *Costacopluma* is *C. concava,* from the Coniacian Arugu Limestone of Nigeria (Collins and Morris, 1975).

LOCALITY

Crab remains reported herein were found by F. J. Vega and E. Centeno during a winter field trip to northern Guerrero, Mexico, in 1989. The studied area is located 125 km south of Mexico City (Fig. 1), near the borderline between the states of Puebla, Morelos and Guerrero. The most important nearby town is Atenango del Rio, Guerrero. Access from Mexico City is via Highway #95, Mexico-Acapulco. About 5 km beyond Iguala, Guerrero, a crossroad leads to Atenango del Rio. From this point, a dirt road to the northeast passes beside Texmalac. About 4.5 km beyond Texmalac, a roadcut on the right side (Fig. 2) exposes bright brown marls that contains shell fragments, plant debris, micromolluscs, and the little crab molds. These sediments have been provisionally assigned to the Mexcala Formation. The locality is registered in the Locality Catalogus of the Museo de Paleontologia of the Instituto de Geologia at the Universidad Nacional Autónoma de Mexico (UNAM) under number IGM-2448.
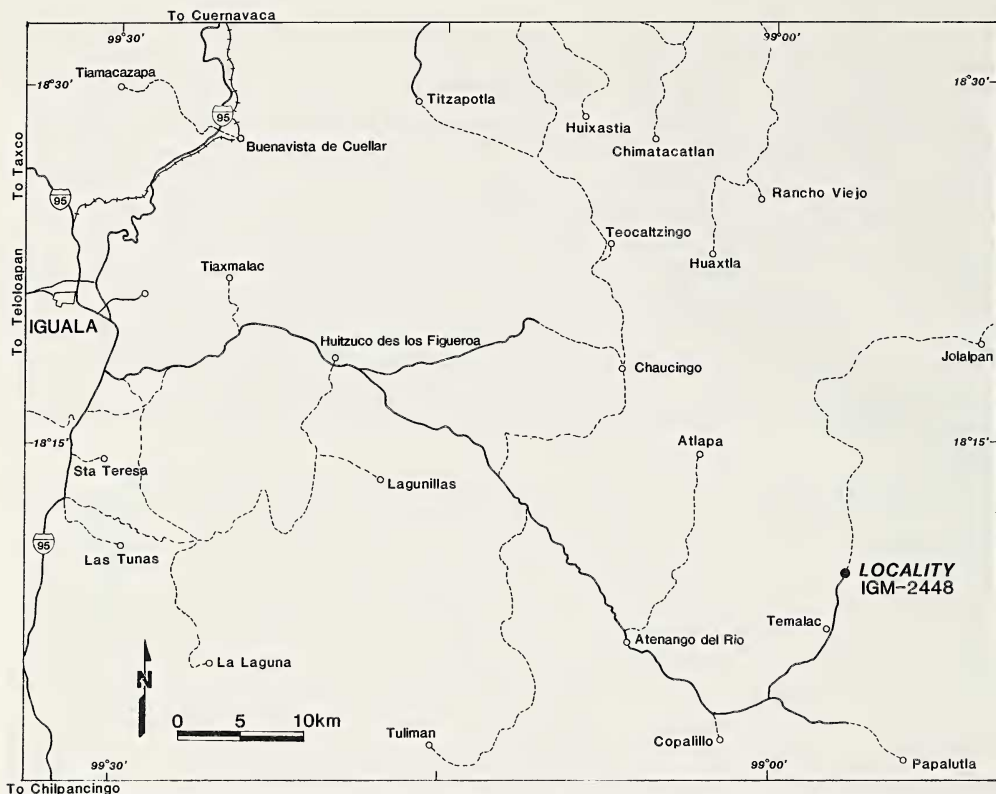
Fig. 2.—Detailed locality map of collecting site in the Mexcala Formation (Loc. IGM-2448), where material was collected, northeast from Atenango del Río, Guerrero.

STRATIGRAPHY AND PALEOENVIRONMENT

The Mexcala Formation was defined by Fries (1960:72) based upon the type section proposed by Bohnenberg-Thomas (1955) for a flysch sequence composed of 1220 m of rhythmic alternation of coarse and fine clastics that crop out at the edge of Río Mexcala, near the town of the same name in Guerrero. Lithologically, the Mexcala Formation exhibits lateral and vertical variation, although the basal portion consists of dark limestones, siltstones and mudstones that owe their color to a high organic content. Sandstones become more frequent toward the top of the formation and conglomerates mark the upper limit of the unit. The Mexcala rests conformably upon the Cuautla Formation, which is composed of limestones that become more arenaceous at the top, near the base of the Mexcala. Erosion has removed the upper portions of the Mexcala Formation in most outcrop areas, but in central Guerrero a continental sequence of red conglomerates rests unconformably upon the Mexcala (Lopez-Ramos, 1983). The Tetelcingo Formation, of apparent Maastrichtian age, rests unconformably upon the Mexcala Formation at Tetelcingo, 40 km west of Texmalac (Ortega-Gutiérrez, 1980). Davila-Alcocer (1974) subdivided the Mexcala Formation into three members, based upon the following vertical lithologic variations (from base to top): 1) calcareous siltstones and mudstones; 2) mudstones and sandstones; and 3) sandstones and conglomerates. Subsequently, Cserna et al. (1980) studied the Mexcala Formation in the

basin of the high Rio Balsas, Guerrero and Michoacan. They noticed that the contact between the Cuautla and Mexcala formations became unconformable to the east. Based on a lithologic and biostratigraphic analysis, they proposed that the Laramide orogenic event affected Mexcala deposition. Gonzalez-Pacheco (1988) subdivided the Mexcala Formation in eastcentral Guerrero into two members (shallow and deep members), based upon very different lithologic characteristics from those described for the type section.

Bohnenberg-Thomas (1955) found *Didymotis* cf. *D. trinidadensis* at the base of the Mexcala in the type section. This bivalve is indicative of an early Coniacian age, although Böse (1923) assigned those forms to species of *Inoceramus* of Turonian age. Microfossil analysis suggests a Turonian age for the base of the Mexcala Formation (Lopez-Ramos, 1983). Davila-Alcocer (1974) found several ammonite species that confirm a Coniacian age for the Mexcala in the central portion of Guerrero. He also found, further to the east, *Tissotia* sp., *Placenticeras* sp. (Gonzalez-Arreola, 1977), and *Anchura* cf. *A. umbrana, Turritella shuleri, Trochus (Tectus) texanus* (Perrilliat-Montoya, 1974), all indicative of a Senonian age. Alencaster (1980) reported several gastropod species indicative of a Maastrichtian age from the same unit in which the crabs described herein were collected. Gonzalez-Pacheco (1988) assigned a Turonian–Coniacian age to his two members and suggested that the sediments containing fossil crabs are from the upper portion of the Mexcala Formation, or his "deep Member," from which he measured 255.5 m of alternating siltstones and sandstones.

Flysch deposits of the Mexcala Formation are indicative of turbiditic sedimentation in marginal basins with moderate depth (Lopez-Ramos, 1983). Deposition began in the Turonian, when the first pulsations of the Laramide orogeny caused erosion of positive elements to the west and deposition of clay and sand that filled the basins to the east as orogeny continued (Ontiveros, 1973). For this reason, the Mexcala Formation becomes younger and shallower to the east. The Mexcala Formation may be as young as Tertiary in some areas.

Fossil crabs were found in light brown marls that rest just above the angular discordance that separates the underlying Cuautla Formation from the Mexcala Formation. Intense deformation makes it difficult to measure an entire section at the collecting site, but a composite sequence is estimated to be 260 m thick (Fig. 3). Associated fauna includes some dinoflagellate cysts, planktonic and benthic foraminifera, corals, gastropods, bivalves, cephalopods, annelids, crustacean chelae, echinoderms, indeterminate fish remains, shark teeth, and indeterminate bones. Also included are plant fragments, palynomorphs and kerogenic material of lignitic type. Excellent preservation of delicate molluscan shells, absence of cross-bedding, and the nature of the fossil assemblage suggest a low energy environment in a shallow platform setting. This conclusion opposed other paleoenvironmental interpretations for deep water environments for these deposits (Gonzalez-Pacheco, 1988)

The tectonic evolution of this portion of southern Mexico suggests that these sediments remained in a platform environment until diagenesis. Palynomorphs associated with the fossil crabs suggest tropical habitat in a coastal humid–hot climate (Martinez-Hernandez, E., personal communication). Some of these palynomorphs include the spores *Stereisporites* sp., *Acanthotriletes* sp. (abundant), *Camarozonosporites* sp., *Heliosporites* sp., *Gleicheniidites* sp.; gymnospermae pollen, *Araucariacites* sp., *Classopollis* sp. (abundant), *Ephedripites* (abundant); and angiosperm pollen, *Alnipollinites* sp.
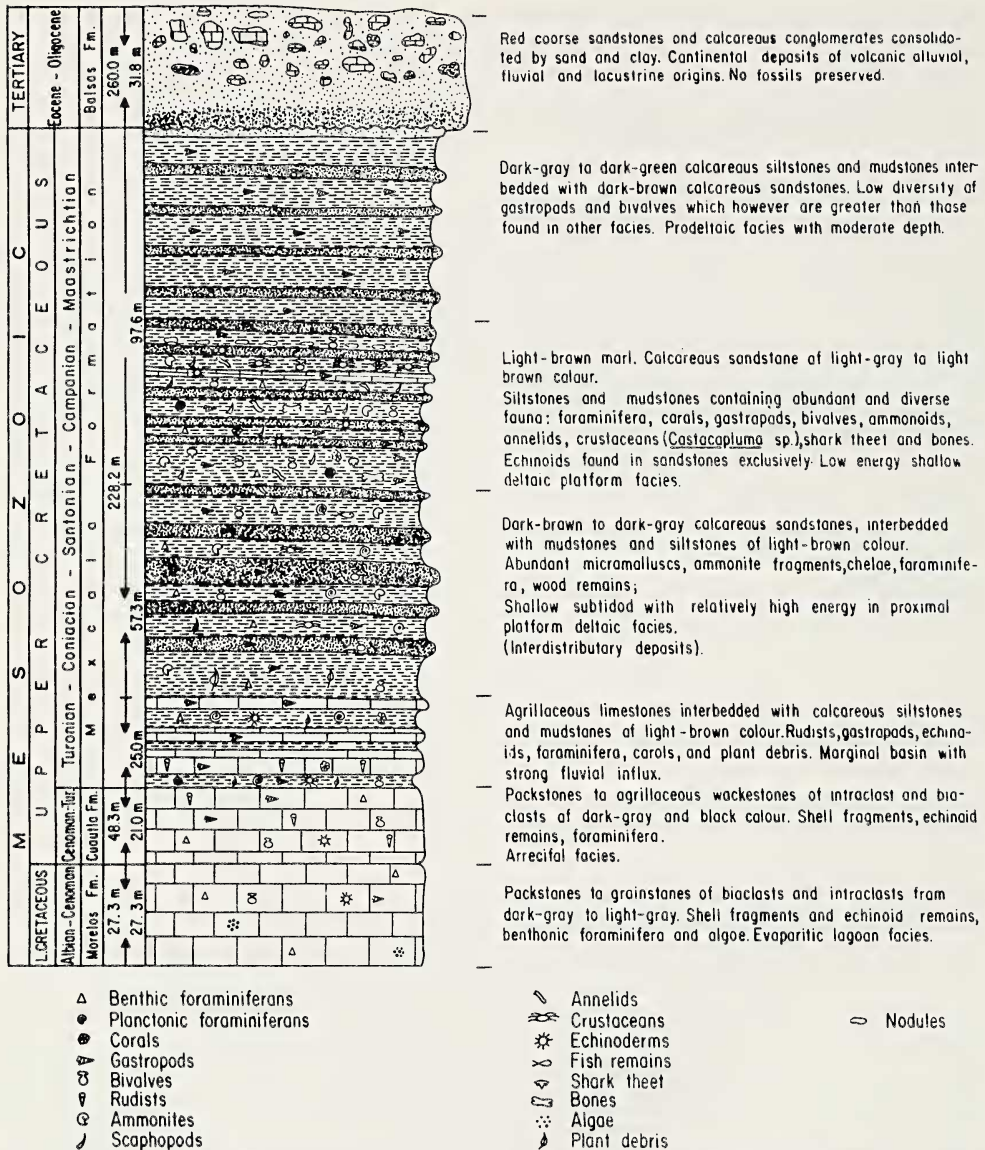
Column lithologic descriptions (right of column):

Red coarse sandstones and calcareous conglomerates consolidated by sand and clay. Continental deposits of volcanic alluvial, fluvial and lacustrine origins. No fossils preserved.

Dark-gray to dark-green calcareous siltstones and mudstones interbedded with dark-brown calcareous sandstones. Low diversity of gastropods and bivalves which however are greater than those found in other facies. Prodeltaic facies with moderate depth.

Light-brown marl. Calcareous sandstone of light-gray to light brown colour.
Siltstones and mudstones containing abundant and diverse fauna: foraminifera, corals, gastropods, bivalves, ammonoids, annelids, crustaceans (Costacopluma sp.), shark theet and bones. Echinoids found in sandstones exclusively. Low energy shallow deltaic platform facies.

Dark-brown to dark-gray calcareous sandstones, interbedded with mudstones and siltstones of light-brown colour.
Abundant micramolluscs, ammonite fragments, chelae, foraminifera, wood remains;
Shallow subtidad with relatively high energy in proximal platform deltaic facies.
(Interdistributary deposits).

Agrillaceous limestones interbedded with calcareous siltstones and mudstones of light-brown colour. Rudists, gastropods, echinoids, foraminifera, corals, and plant debris. Marginal basin with strong fluvial influx.
Packstones to agrillaceous wackestones of intraclast and bioclasts of dark-gray and black colour. Shell fragments, echinoid remains, foraminifera.
Arrecifal facies.

Packstones to grainstones of bioclasts and intraclasts from dark-gray to light-gray. Shell fragments and echinoid remains, benthonic foraminifera and algae. Evaporitic lagoon facies.

Legend:

△ Benthic foraminiferans
● Planctonic foraminiferans
❋ Corals
🐚 Gastropods
🐚 Bivalves
ᚦ Rudists
Ⓖ Ammonites
♪ Scaphopods

❧ Annelids
🦐 Crustaceans
❋ Echinoderms
✕○ Fish remains
✓ Shark theet
⊏⊐ Bones
∴ Algae
🌿 Plant debris

⌐ Nodules

Fig. 3.—Composite stratigraphic column of Atenango del Río area. Fossil content distribution and paleoenvironmental interpretation is shown along with a brief description of lithology.

Facies changes in relatively short distances are observed in the Mexcala Formation, and an estimated high rate of sedimentation of kerogenic-rich material, suggest a direct fluvial influx over a small deltaic platform. It appears that *Costacopluma* spp. preferred such environments, as *C. concava* was found in Upper Cretaceous deltaic sediments of Nigeria (Reyment, 1956). *Costacopluma concava* from north India was found in sediments that represent a shallow marine environment with a minor amount of terrigenous material derived from the Indian Craton (Gaetani et al., 1983:101). *Costacopluma mexicana* is abundant in lower delta-platform deposits of the Potrerillos Formation (Difunta Group) in Maas-

trichtian northeastern Mexico (Vega, 1988; Vega and Perrilliat, 1989). Paleocene sandy limestones of Senegal contain *C. senegalensis*. A paleoenvironmental analysis of the Senegal sequence suggests a well-aerated sea with a maximum depth of 50 m (Tessier, 1952). Based upon the associated fauna of molluscs, bryozoans and echinoderms (Gorodisky and Remy, 1959:315), a shallow marine environment with low clastic influx is indicated. Recent petrographic analysis and study of primary structures observed in the field (Gonzalez-Pacheco, 1989) reinforces the deltaic paleoenvironmental interpretations for the part of the Mexcala Formation under consideration here.

Alencaster (1980) listed 15 gastropod species recovered from the unit that contains fossil crabs. These molluscs are suggestive of a Maastrichtian age and are also known from the Maastrichtian of Tennessee, Mississippi, Alabama, Georgia and Texas, the Owl Creek, Ripley, Kemp, Corsicana, and Nacatoch formations respectively. Maastrichtian formations in northeastern Mexico where some of these species have been found include the Cardenas Formation in San Luis Potosi, and the Potrerillos Formation in Nuevo Leon. All gastropod species reported by Alencaster (1980) fall into the *Exogyra costata* Say, and *Sphenodiscus pleurisepta* (Conrad) zones. Gastropod species associated with the Guerrero retroplumid specimens are: *Haustator trilira* (Conrad), *Pugnellus densatus* Conrad, *Bellifusus curvicostatus* (Wade), *Gyrodes supraplicatus* (Conrad), *Deussenia ripleyana* Harbison, *Cerithium weeksi* Wade, and *Euspira rectilabium* (Conrad). Most of these species were reported for Maastrichtian deposits of the Atlantic and Gulf Coastal Plains (Wade, 1926; Gardner, 1916; Gabb, 1860; Conrad, 1852, 1858, 1860, 1869; Imlay, 1937; Wolleben, 1977; Stephenson, 1941; Myers, 1968; Morton, 1829; and Sohl, 1960). The Potrerillos Formation (McBride et al., 1974) contains *Costacopluma mexicana* associated with *Haustator trilira, Pugnellus densatus, Deussenia ripleyana, Gyrodes rotundus* Stephenson, and *Bellifusus* sp. (Vega and Perrilliat, 1990). All are indicative of a Maastrichtian age (Jablonski, 1979). Based upon the biostratigraphic range of 18 gastropod and bivalve species, Vega (1988) proposed a late Maastrichtian age for the lower siltstone member of the Potrerillos Formation. Consequently, it is proposed that *Costacopluma mexicana* inhabited shallow deltaic facies in northeastern Mexico during that time. Thus, faunal correlations with other Upper Cretaceous deposits of northeastern Mexico and southeastern United States suggest a Maastrichtian age for the Mexcala Formation strata containing *Costacopluma bishopi* n. sp.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1803
Section Thoracotremata Guinot, 1977
Superfamily Ocypodoidea Rafinesque, 1815
Family Retroplumidae Gill, 1894
Genus *Costacopluma* Collins and Morris, 1975
***Costacopluma bishopi*,** new species
(Fig. 4)

Type and referred material.—Eight carapaces were collected from the Mexcala Formation in Guerrero (loc. IGM-2448), southern Mexico. Seven are internal molds of juvenile exuviae, of which five are complete, and one is an incomplete mold of the exterior of a juvenile carapace. Seven samples are included in the paleontological collection of the Museo de Paleontología of the Instituto de Geo-
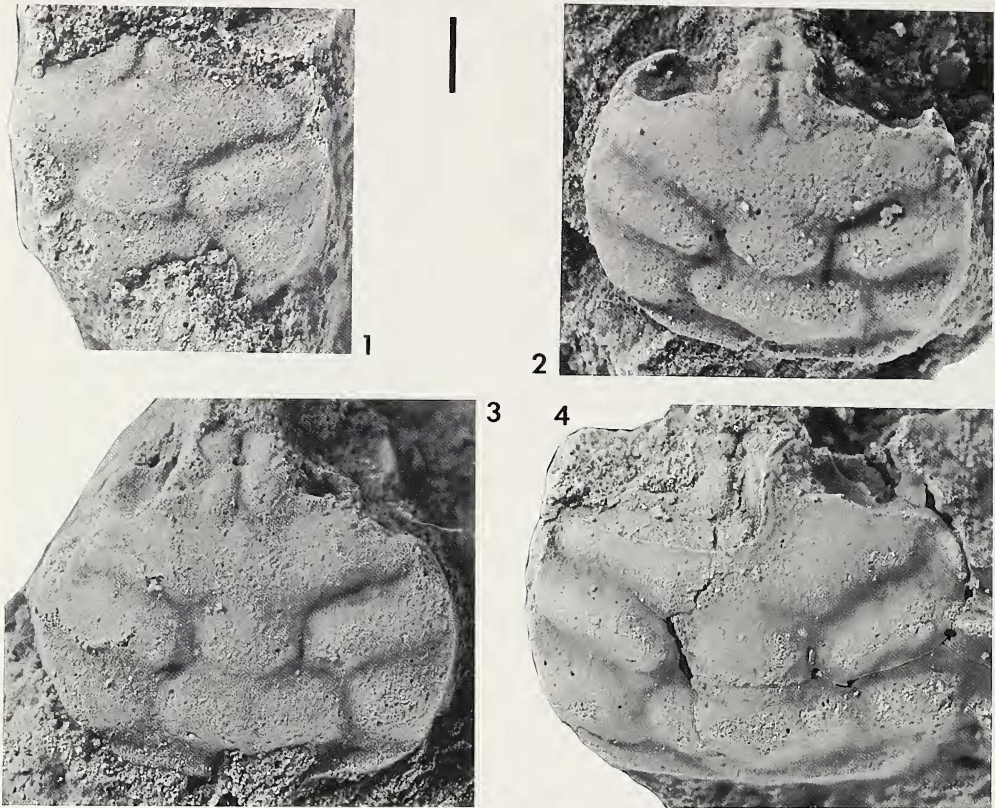
Fig. 4.—*Costacopluma bishopi* n. sp. from the Mexcala Formation, Maastrichtian, of Guerrero, Mexico, Loc. IGM-2448. 1, Paratype, IGM-5227; 2, Paratype, IGM-5225; 3, Holotype, IGM-5226; 4, Paratype, IGM-5224; Scale bar equals 1 mm.

logia, Universidad Nacional Autónoma de México, with catalog numbers IGM-5224 to IGM-5230. One paratype specimen, CM 34963, is deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. The holotype, IGM-5226 and three paratypes, IGM-5224, 5225, and 5227, are illustrated (Fig. 4).

Description.—Carapace transversely suboval, with three transverse arched ridges. Areas between ridges deeply concave. Length ⅔ of maximum width, which is at the level of mesobranchial lobes. Lateral margins inclined almost at right angles to dorsal surface. Anterolateral margins short, with a rounded angle situated ⅓ length from front. Posterolateral margins rounded, slightly convergent ending in a rounded angle that passes to posterior margin which is ⅓ maximum width. Posterior margin raised, with small blunt protuberances at posterolateral angles. Lateral margins delineated by elevated border that extends anteriorly from metabranchial lobes and becomes sharper at level of mesobranchial lobes. Edge continuous along posterior and lateral margins. Frontoorbital margin straight, about ⅘ greatest width. Rostrum short, subquadrate, bluntly terminated, sulcate to mesogastric lobe. Upper orbital margin divided into two nearly equal parts by short, sharp spine, situated ¼ of width from external orbital margin, defined by sharp conspicuous spine that projects beyond front.

Absence of cuticle prevents observation of carapace ornamentation except on part of one specimen, a mold of the exterior.

Cervical groove transversely sinuous, extending from marginal notch behind tip of protogastric lobe and deepening toward narrower portion of mesogastric lobe, continuous and becoming shallower in nearly straight line toward the base of mesobranchial lobe. Anterior transverse ridge formed by protogastric and mesogastric lobes. Tips of protogastric lobes very near, but not reaching, anterolateral margins, lobes slightly sinuous and widening toward narrow portion of mesogastric lobe, which is

Table 1.—*Measurements taken on juvenile specimens of* Costacopluma bishopi *n. sp.*

Catalogue number	Length (mm)	Width (mm)	L/W ratio
IGM-5224	3.9	5.5	0.70
IGM-5225	3.3	4.9	0.67
IGM-5226	3.2	4.7	0.68
IGM-5227	2.9	4.2	0.69
CM 34963	3.4	5.2	0.65
x̄	3.34	4.9	0.678

semioval, situated axially at midlength. Medial transverse ridge formed by fusion of epibranchial and mesobranchial lobes, extends from lateral margin posteromedially to base of mesogastric lobe. Touching lateral margin, lateral tip of ridge intercepts lateral margin of carapace, forms a ridge that extends anteriorly to base of external orbital spine. Crests of epibranchial and mesobranchial lobes prominently rounded, slightly wider toward base of mesogastric lobe. Posterior transverse ridge corresponds to metabranchial lobes and cardiac region. Metabranchial lobes blunt ridges slightly inclined toward posterolateral margins widest at margin of carapace, lobes shorter and more rounded than mesobranchial lobes. Cardiac region half of greatest width.

Abdominal and frontal regions not preserved.

Measurements, in mm, are given in Table 1.

Etymology. — The species name honors Dr. Gale Bishop, Georgia Southern College, a well-known student of Cretaceous crabs.

Discussion. — In this paper, the Retroplumidae is considered to contain *Retropluma, Bathypluma, Archaeopus, Cristipluma,* and *Costacopluma.* Saint Laurent (1989) erected the superfamily Retroplumoidea, subdividing it into two families — the Costacoplumidae for the Eurafrican fossil representatives, *Costacopluma* spp., and *Retrocypoda* spp.; and the Retroplumidae for the Recent species, *Retropluma* spp. and *Bathypluma* spp. She also suggested that *Archaeopus* and *Cristipluma* be assigned to families outside the Retroplumoidea. St. Laurent did not provide a definition for the Costacoplumidae. Examination of original descriptions of the genera known only from the fossil record as well as specimens representative of most of the described species leads us to the conclusion that there is no basis for making this distinction. All have generally flattened, rectilinear to ovoid carapaces, distinct borders, and all exhibit variable degrees of development of three transverse carinae. Therefore, we include all five genera within the Retroplumidae. The distinction between the genera is readily expressed in the following key to the genera. Genera with extant representatives are indicated in boldface type.

Key to the genera of Retroplumidae

1. Rectangular to hexagonal carapace; anterior and posterior carinae most strongly developed 2

1'. Subrectangular to ovoid, median carina and anterior or posterior carina most strongly developed 3

2. Carinae with narrow crests; lateral and anterolateral protuberances developed as nodes; greatest width at anterolateral node; posterior margin wide . . . . ***Retropluma***

2'. Carinae with broadly rounded crests; lateral and anterolateral spines present; greatest width at median spine; posterior margin wide . . . ***Bathypluma***

3. Anterior and median carinae best developed; carinae broadly to narrowly crested; lateral margins without spines, posterior margin narrow . . . . . .
. . . . *Costacopluma*
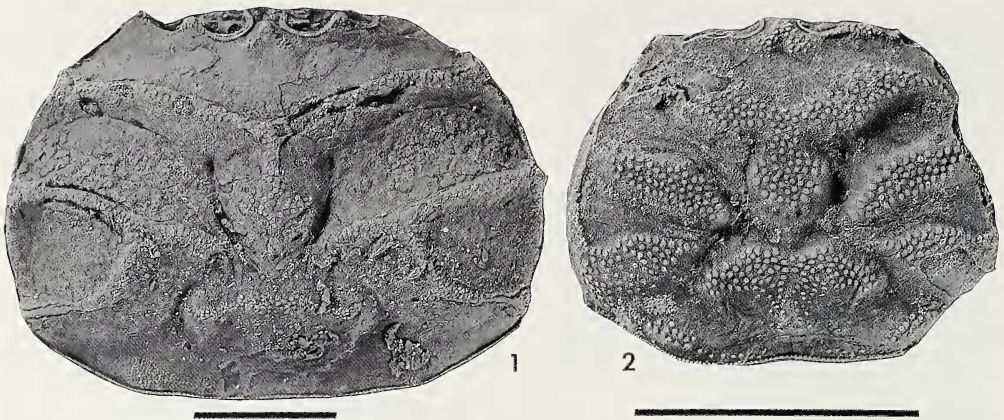
Fig. 5.—Species of *Costacopluma* from Upper Cretaceous of Africa and America. 1, *Costacopluma concava* Collins and Morris, KSU 4882, from the upper Campanian of Nigeria; 2, *C. mexicana* Vega and Perrilliat, KSU 4, from the upper Maastrichtian of Northeastern Mexico. Scale bars equal 1 cm.

3'. Median and posterior carinae best developed; carinae broadly to narrowly crested; lateral margins with or without spines; posterior margin variable
.... 4

4. Subrectangular; carinae with rounded crests; lateral margin spinose; posterior margin narrow .... *Archaeopus*

4'. Ovoid to subhexagonal; carinae with narrow crests; lateral margins without spines; posterior margin wide .... *Cristipluma*

Within *Costacopluma,* differences between species are based upon carapace outline, degrees of development of transverse carinae, and ornamentation of the dorsal shield. The differences between *Costacopluma mexicana* and the Guerrero specimens lie chiefly in carapace outline and shape of the dorsal regions. As in *C. concava,* the widest part of the carapace of *C. mexicana* is slightly anterior to the level of the metabranchial lobes (Fig. 5). The anterolateral margins of *C. mexicana* are comparatively longer and more inclined than those of *Costacopluma bishopi.* The frontoorbital margin of *C. mexicana* is about ½ the maximum width whereas it is about ¾ the maximum width in *C. bishopi.* The posterior margin of *C. mexicana* is ¾, while that of the Mexcala specimens is ⅓ the maximum width. The posterior margin in both forms is nearly straight. The rostrum of *C. mexicana* is trapezoidal, while in the specimens from Guerrero it is subquadrate. The supraorbital spine is less prominent and more rounded in *C. mexicana.* This spine lies nearer to the external orbital spine in *C. mexicana* and the external orbital spine is not as prominent in *C. mexicana* as it is in *C. bishopi* from Guerrero. The anterior ridge of *C. mexicana* is more arched. The crests of protogastric, mesogastric, mesobranchial, and metabranchial lobes of *C. mexicana* are nearly flat. This feature is observed even in juvenile specimens (Fig. 6). The metabranchial lobes of *C. mexicana* are nearly parallel to the posterior margin and are wider than those observed in the Guerrero specimens. The mesogastric lobe and cardiac region are very similar in outline in the two forms.

With respect to *C. concava,* Collins and Morris (1975:826) stated, "There is a tendency for the ridges to become sharper as growth advances . . . ." The sizes of their specimens ranged from 6.9 mm to 26.0 mm across the carapace. The figured
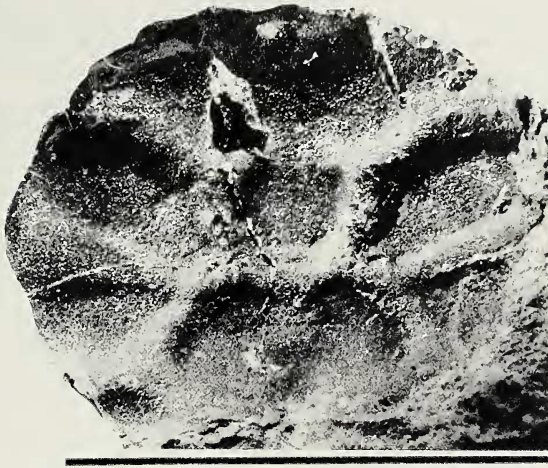
Fig. 6.—Juvenile specimen of *Costacopluma mexicana* Vega and Perrilliat, from the Maastrichtian Potrerillos Formation (Difunta Group), in northeastern Mexico. Note flat crests of protogastric, epigastric, mesogastric, mesobranchial, metabranchial, and cardiac regions, very similar to adults. Photographed unwhitened. Scale bar equals 1 cm.

specimen of *C. senegalensis* by Remy (1959) has a maximum width of 36.7 mm. Maximum width in *C. mexicana* ranges from 11.2 mm to 26.7 mm, and in *Costacopluma bishopi* from Guerrero from 4.2 mm to 5.5 mm. These specimens are interpreted as juveniles; they are the smallest examples of this genus ever reported (Fig. 7). The lack of preserved cuticle in our samples makes it difficult to make detailed comparisons with other species. However, the smallest specimen of *C. mexicana* (Fig. 6) has well-defined morphological characteristics of the carapace of adults. This suggests that the flat crests of lobes in this species developed at a very early ontogenetic stage. Preservation of our material as molds of the interior makes it even more difficult to make species-level comparisons. However, the shape of crests of *Costacopluma bishopi* and comparison of juvenile and adult specimens of *C. concava* and *C. mexicana* allows us to propose that the Mexcala *Costacopluma* represents a new species closely related to *C. mexicana.* In *C. concava,* carinae become sharper as growth advances; thus, it is probable that the lobes of the Guerrero Retroplumidae were not as flattened in adults as in *C. mexicana.*

PHYLOGENY AND PALEOBIOGEOGRAPHY

Morphological analysis of the four species of *Costacopluma* suggests that they could be subdivided in two phyletic groups. The African group contains *C. concava* and *C. senegalensis* and is characterized by: 1) narrow transverse ridges with steep slopes; 2) broad, concave areas between ridges; 3) narrow, nearly straight protogastric lobes which are almost parallel with respect to the frontoorbital margin; 4) rhombic mesogastric lobe, longer than wide; 5) long, narrow mesobranchial ridges; and 6) short, narrow metabranchial areas, inclined toward posterolateral margins. Although carapace size could be facies controlled, both African species are larger than the American forms. The American group includes *Costacopluma mexicana* and *Costacopluma bishopi,* and is distinguished by: 1) broad transverse ridges, with rounded to flattened crests and gentle slopes; 2) concave, narrower
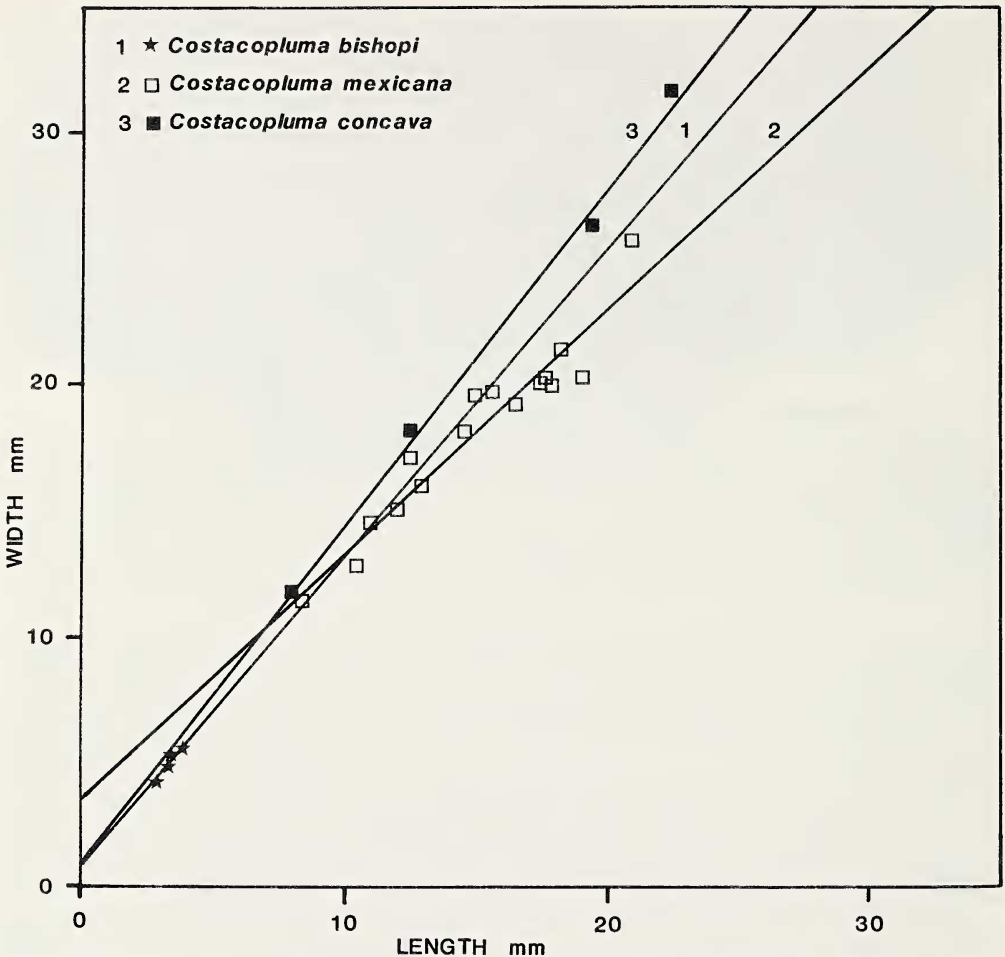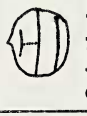
Fig. 7.—Plots of length/width regression lines for *Costacopluma mexicana* Vega and Perrilliat (16 specimens); *C. concava* Collins and Morris (four specimens); and *Costacopluma bishopi* n. sp. from the Mexcala Formation (five specimens).

areas between ridges; 3) protogastric lobes which are narrow at the tip near the anterolateral margins but wider and sinuous toward the center of the carapace; 4) oval mesogastric lobe, wider than long; 5) mesobranchial ridges are narrow at both ends and wider centrally; and 6) broad metabranchial lobes that are nearly straight, wider at the contact with posterolateral margins and narrowing near the cardiac lobe; posterior ridge almost parallel to posterior margin. The morphology of the carinae is among the most significant characters in definition of species throughout the Retroplumidae. Therefore, the American species would be the more primitive in that the topography of the dorsal carapace tends to be more rounded and the demarcation between carinae and intervening areas more subtle than in the African species. Extant retroplumids, *Retropluma* spp. and *Bathypluma* spp., exhibit straight carinae with narrow crests. These morphological characters were first observed in the African forms of *Costacopluma* in the Late Cretaceous and are accentuated in the Tertiary species of *Retropluma*.

The African group ranges from Coniacian to Paleocene of eastern Africa, and occurs in the Maastrichtian of north India. Collins and Morris (1975:827) stated that *C. senegalensis* from the Paleocene of Senegal could be a direct descendant of *C. concava* from the Coniacian–?Maastrichtian of Nigeria. The American group is represented only in the Maastrichtian of Mexico. This could be a consequence of lack of Tertiary marine deposits in some sequences in southern Mexico. Where Tertiary sediments are present, as they are in northeastern Mexico, they represent continental environments in which it is improbable to find fossil crabs. Older units remain to be prospected.

Rathbun (1908) erected *Archaeopus* based upon the Coniacian–Maastrichtian species *A. antennatus* and *A. vancouverensis* from California and Canada, and noted that the development of transverse carinae, and general outline was a basis for recognizing close affinities with *Retropluma*. Beurlen (1930) included the Retroplumidae and Ocypodoidae in the section Ocypodoida. Glaessner (1960) discussed the validity of this relation in light of the sparse fossil record. At that time, the oldest known representatives of the Retroplumidae were middle Eocene (Glaessner, 1969). Collins and Morris (1975) erected *Costacopluma* and discussed arguments of Via (1957) to support the African origin of this family. Via suggested that one retroplumid lineage remained in America, represented by *Archaeopus* on the Pacific Slope and *Ophthalmoplax* in the Gulf of Mexico and northern South America, while another lineage migrated eastward, eventually becoming the rootstock of modern representatives of the family. Collins and Morris (1975) opposed this idea, arguing that the oldest representatives of the Retroplumidae were found in the Coniacian of Africa, and that *Ophthalmoplax comancheensis* Rathbun from the Albian of Texas was poorly represented by fingers and chelae and, at least by inference, should not be included within the family. They noted that the presence of ocypodid *Goniocypoda tessieri* Remy, reinforced an African center of evolution for ocypodids, and that an eastward migration during the Tertiary through southern Europe gave rise to the modern representatives. Guinot (1978) considered the fossil record of Retroplumidae too poor to recognize phylogenetic relations of this family, and suggested that the study of larval morphology might be the tool necessary to elucidate affinities. Via (1982) revised fossil and Recent occurrences of the Ocypodoidea and reiterated his previous view (Via, 1957, 1959, 1969) regarding an Early Cretaceous American origin and subsequent eastward migration during Late Cretaceous and Tertiary time. He recognized two phylogenetic trends (Via, 1982:118): 1) populations that gradually adapted to deep water and subsequently gave rise to modern forms of *Retropluma,* inhabiting Indo-Pacific seas, with a Cretaceous *Ophthalmoplax*-like ancestor; and 2) a second group of species still inhabiting coastal environments similar to Recent forms of *Macrophthalmus* Desmarest, that could be direct descendants of Eocene *Retrocypoda,* the possible precursors of the Macrophthalminae. Via also suggested that this subfamily provides the best evidence to understand the phylogenetic relations between the Ocypodidae and Retroplumidae. Bishop (1983:427–428) stated that, "If *Ophthalmoplax* is removed from the Retroplumidae, the evolutionary development of the family becomes obscure, since *Archaeopus* (from the Campanian–Maastrichtian of the Pacific Slope), *Cristipluma* (from the Late Cretaceous of the Mississippi Embayment), *Costacopluma* (from the Coniacian–Paleogene of West Africa), and *Retropluma* (from the Eocene–Holocene in Spain, Italy, and Indo-Pacific) do not clearly fall into a pattern of development that makes a significant amount of sense." He also postulated that *Archaeopus* could have the ancestral

morphology of retroplumids as the ornamentation of its carapace seems to be less specialized, and that *Costacopluma* and *Retropluma* "seem to be closely related lineages which developed in two geographic centers" (1983:428). Saint Laurent (1989) suggested that *Archaeopus antennatus* was not a retroplumid and that reexamination of the specimens of this species would reveal its systematic position.

Ophthalmoplax is considered to be a portunid crab with a flattened propodus on P5 as well as shape and ornamentation of the carapace that exclude it from the Retroplumidae and suggest inclusion in the Carcineretidae. This means that the oldest known retroplumids are species of *Archaeopus* and *Costacopluma*. Via (1980:64) considered *Archaeopus rathbunae* Beurlen from the Early Cretaceous of Brazil to be the oldest representative of his shallow-environment-trend group. It was based on one carapace that resembles those of the Carcineretidae rather than the Retroplumidae. He also compared this crab with *Goniocypoda sulcata* Carter, from the Early Cretaceous of England, which he included in *Archaeopus,* and which was based on an incomplete specimen (Carter, 1898) that seems to have affinities with the Xanthidae. Glaessner and Rao (1960) restudied the type of *A. sulcatus* and concluded that it was, in fact, a *Macrophthalmus* subfossil. Beurlen's suggestion about synchronous distribution of *Archaeopus* in America and Europe during the Albian is improbable, as the adaptive radiation of the Brachyura had just begun at that time. Thus, if *Ophthalmoplax* is a carcineretid crab, and if the "Early Cretaceous" *Archaeopus sulcatus* has been misidentified, Via's scheme of phylogeny (Via, 1980:fig. 2) is open to serious question. He stated that (p. 11) "Le famille Retroplumidae aurait eu une origine américaine et ses représentants ont fourni des restes fossiles (*Ophthalmoplax* et *Archaeopus* en Amérique, *Costacopluma* en Afrique) á partir du Crétace inferieur (Albien)." Via considered the presence of *Retrocypoda* in the Paleocene of Brazil to be a blind branch of evolution of the Retroplumidae in America. He based this conclusion on a report of this genus by Beurlen (1965) who cited the presence of *Retrocypoda* from the Maria Farinha Formation of Brazil, but neither figured specimens nor gave a description (p. 272). However, the morphology of the dorsal region of the carapace in *Retrocypoda* does not fit retroplumid features. For this reason, this genus is treated as a neighbor taxon of the retroplumids, which probably was differentiated from the retroplumid lineage in the Paleogene, as was proposed by Via (1980).

Fig. 8 is an alternative scheme for the phylogeny and evolution of the Retroplumidae based upon exclusion of some taxa and inclusion of *Costacopluma* in America. The Retroplumidae is restricted to *Archaeopus, Bathypluma, Costacopluma, Cristipluma,* and *Retropluma.* Figured specimens of *A. vancouverensis* by Bishop (1986:fig. 10c, d), clearly demonstrate affinities with *Costacopluma,* making it probable that the Retroplumidae originated in North America. Bishop (1983:429) wrote, "The presence of a retroplumid in the Coon Creek Formation was unexpected. Not only does this record significantly extend the geographic and stratigraphic range, but it is also paleoecologically anomalous, being a deep-water crab preserved in shallow water sediments. This Late Cretaceous record places *Cristipluma* in close stratigraphic and geographic proximity to *Archaeopus,* a taxon

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Fig. 8.—Proposed phylogenetic and evolutionary diagram for Retroplumidae, omiting some genera previously included in this family and considering new fossil representatives. (After Via, 1982.)

considered to be near the base of the ocypodoidid adaptive radiation (Via, 1980; Glaessner, 1980)." An American center of dispersion for the Retroplumidae was proposed by Via and Cals (1979). These authors proposed three migrational directions: 1) to the northeast, across the Tethys; 2) toward the South Atlantic Ocean; and 3) to the west, toward Panama and Colombia. Saint Laurent (1989) rejected evidence of an American origin for the Retroplumidae, arguing that the identification of the American representatives of this family was doubtful, and that the retroplumid migration across the proto-Atlantic should have produced a diversification, which is not consistent with the recent homogeneity of the group inhabiting Indo-Pacific seas. The broad distribution of *Costacopluma* during Maastrichtian time (North America, southwest Africa, and northern India) is sufficient evidence to propose that the diversification of the group was at the species level, even across the proto-Atlantic (*C. mexicana* and *C. bishopi* in North America, and *C. concava* in Africa and India). Late Cretaceous American representatives of the Retroplumidae were discussed by Saint Laurent (1989), who excluded *Archaeopus antennatus, A. vancouverensis,* and *Cristipluma mississippiensis* from the retroplumid lineage, based upon morphologic and preservational arguments. Presence of *Costacopluma mexicana* in Nueva Leon and *Costacopluma bishopi* in Guerrero confirms an American center of evolution for the Retroplumidae, with *Archaeopus* at the base. Representatives of *Costacopluma* and *Cristipluma* were adapted to marginal marine environments of soft-sediment before Maastrichtian time. As mentioned above, the presence of *C. concava* in the Coniacian of Africa does not imply that this genus originated there and subsequently migrated to America. It now seems more probable that the genus originated in America during the Late Cretaceous and subsequently migrated to West Africa, and then to India.

Hines (1986) cited a 29-day larval period for representatives of the Ocypodidae and emphasized the anomalous larval morphology and behavior of this family. Referring to brachyuran species, he stated that (p. 450), "among marine species there was no significant relationship between extent of the range and duration of the zoeal period or duration of the total larval period . . . ." The larval period of extant species of retroplumids is unknown, but whatever it may be, it seems that the duration of larval activity need not play an extremely important role in retroplumid species distribution. Garth (1966) noted that in some brachyuran pelagic larvae, the duration of instars can be prolonged, with obvious possible effects on distribution. The crossing of modern Ocypodidae across the East Pacific Barrier could occur via island hopping (Crane, 1975). This may be the basis for explaining the migration of *Costacopluma* across the Late Cretaceous Atlantic Ocean from America to Africa. Spreading of the Atlantic seafloor at that time generated deep basins, but also created islands along the crest of the mid-Atlantic ridge (Berggren and Hollister, 1974). Several surficial paleocurrent patterns for the Late Cretaceous Atlantic have been proposed (Luyendyk et al., 1972; Berggren and Hollister, 1974; Scheltema, 1986; Barron and Peterson, 1989), and all but the latter suggest current circulation from east to west. The model of Barron and Peterson, however, does include an eastward circulation through Tethys. Thus, island hopping coupled with larval dispersal in eastward-flowing currents seems to be the most parsimonious suggestion to explain the wide distribution of this genus in the western and eastern Atlantic. With respect to the synchronous distribution of *Costacopluma concava* in the Late Cretaceous in west Africa and northern India, Saint Laurent (1989:150) wrote, "Les documents fossiles incon-

testables témoignent de sa présence dans la portion centrale de la Mèsogée crétacée: bassin du Niger à l'ouest, nord de la future peninsule indienne à l'est . . . On peut supposer que leur distribution étendait aussi largement à l est vers le futur océan Indien, alors plus ou moins en communication avec la Paratétys." Post-Mesozoic eastward migration of the Retroplumidae in the Tertiary and Quaternary in Spain and Italy could be explained by lateral displacement of populations along the continental margins and gradual adaptation to deep waters. Absence of *Costacopluma* in Upper Cretaceous shelf deposits of southeastern United States may be due to paleoclimatic differences. The northern limit of the tropical-subtropical zone in America was about at the geographic position of deltas that produced the Difunta Group in northeastern Mexico (Davids, 1966; Berggren and Hollister, 1974). Timing of metamorphosis of some pelagic larvae into littoral crustaceans is partly controlled by characteristics of the water. The molts to postpelagic stages apparently are triggered by chemical factors occurring near land (Crane, 1975).

Late Cretaceous decapod assemblages in the United States in shallow soft-sediment environments were often dominated by *Dakoticancer* spp. As stated above, geographic restriction of *Costacopluma* spp. could be a consequence of paleoclimate. Where *Dakoticancer australis* has been found in the same unit as *Costacopluma mexicana* (Vega and Feldmann, 1991), it is much rarer than in Upper Cretaceous deposits of the Western Interior and the Atlantic and Gulf Coastal Plain. *Costacopluma* is the dominant element of decapod assemblages in Upper Cretaceous deposits from Mexico and Nigeria. By Paleocene time, however, *Costacopluma* disappeared from America and was less abundant in West Africa. At the same time, *C. senegalensis* adapted to deeper water conditions. Eocene–Pliocene retroplumids continued to radiate into deeper water. Modern species of *Retropluma* and *Bathypluma* inhabit depths of 50 to more than 600 m in the Indo-Pacific Ocean (Saint Laurent, 1989).

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